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Periodic changes in the weight of the gonads and the spawning cycle of Baltic and Belt Sea cod (G. morhua callarias/G. morhua morhua) in different parts of the Baltic

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PERIODIC CHANGES IN THE WEIGHT OF THE GONADS AND THE SPAWNING CYCLE OF BALTIC AND BELT SEA COD (G. MORHUA CALLARIAS/ G. MORHUA MORHUA) IN DIFFERENT PARTS OF THE BALTIC

by Dr. M. BERNER, Rostock Institute of Deep Sea Fishery and Fish Processing, Department of Baltic Fishery Biology

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The investigations were performed by calculating length-weight relations for the gonads (Table 2) and determining the gonadosomatic indices (Table 3) or percentual changes in the weight of the gonads (Figures 2, 3, 5, 6, and 8). They confirm certain earlier assumptions, e.g., that males attain sexual maturity and ripeness for spawning earlier, and that large codfish of both sexes in the same spawning population finish spawning early, whereas small fish spawning for the first time finish late. For mixed stocks of G. morhua callarias L. and G. morhua morhua L., the gonadosomatic indices reveal an extension of the spawning season and partial differentiation of prespawning shoals and spawners. It must be assumed that both races form their own spawning populations at their characteristic spawning times. The distinct increase of the callarias component in the mixed stocks of the Arkona Sea and Mecklenburg Bay since 1980 has led in both regions to corresponding temporal shifts in the peak spawning season and catches (Table 4).

Introduction

It has been known for a long time that over the course of a year, the maturity cycle can entail considerable changes not only in the weight of the gonads, but also in the total weights of all affected length-groups and ages. Accordingly we may assume that maturity cycles and spawning behavior are already fully researched.

However, partial questions such as the relation between maturity cycles and the length of the fish have usually been studied only for both sexes together, and according to maturity stages rather than by directly weighing the gonads. Thus SIMPSON as late as 1959 (22) could still advocate the general opinion that in the case of North Sea plaice, older fish begin the spawning season, while the younger fish arrive later at the spawning grounds. SIMPSON assumed that the latter were mostly males spawning for the first time. This seems logical, since the males often attain sexual maturity at a lower age and with shorter average lengths, and thus form the bulk of small spawners. However, DE CLERCK and REUSSENS 1982 (14) proved by weighing that it is only among female North Sea plaice that the older fish start the spawning season and the younger fish spawn later. In the case of the males, the young fish spawn first, then the older fish. This has been confirmed by RAUCK's (20) investigations.

Under these circumstances, it seemed advisable to analyze the spawning behavior of the Baltic cod separately for each sex, especially since the material for 1953-1955 from the Arkona Sea yielded certain discrepancies in the seasonal average weights for full and spent fish, which have already been noticed (6, 7), but were not entirely explained.

It should be emphasized at this point that on the present assumptions of fisheries and fishery science the

spawning behavior of our commercial fishes is no longer of purely biological interest, but, e.g., through its close connection with the total weight of fish, it also enters into, and directly affects, questions of evaluating stock and predicting catches. DE CLERCK 1981 (13) showed impressively that predictions based on virtual population analyses as a product of the number of individuals and their average weight can be greatly falsified by the values used for weight. If the fishery is concentrated on a particular fishing season, or if the seasonal fishing intensity changes each year-- we must assume both factors-- then the accuracy of the weight values used is critical. On the other hand, given the seasonal variation of the age-class composition of the catch, and of the values for weight, it is difficult to attain sufficient accuracy within the bounds of possible working procedures. Since the seasonal variation depends preferentially on the spawning behavior of the fish stock and sexes, a better knowledge of spawning behavior may be the key to more accurate estimates of weight values and correct assessment of fish stocks.

Material and Method

Because of the different results from particular regions and times, we attempted to provide a broader basis for this study, and to include in our survey as many Baltic codfish stocks as possible, and sometimes

also the same stocks in different years. The regions and the way in which the material was caught and processed are shown in Table 1. In spite of our efforts to widen the material, especially the temporal limits of the basic data should not be overlooked.

As a rule, when the sex, maturity stage, and length of a codfish were known, its gonads were weighed. Then, to group the material into suitable temporal and spatial categories, the length/weight relation $W = a L^b$ (W = weight, L = length) was computed for the weight of the gonads separately for each sex, using the expanded WTLN program according to ABRAMSON (1). The values computed for 'a' and 'b' are listed in Table 2. With respect to the material from 1953-1955, some additional data regarding the collection of the material are given in (6) and similar length/weight relations are presented --but only quarterly values for both sexes together. The regions listed in Table 2 were either surveyed year-round from 1953 to 1955 and compiled quarterly, or else surveyed for a period of four months during the season in 1971-1978 or in 1981-1984 and compiled, in most cases, monthly.

From the length/weight relations, the mean gonad weights listed in Table 2 were derived for codfish 30-90 cm long, and further processed in two ways. First, the isometric gonadosomatic indices (GSI's) were calculated (Table 3) as proposed by HILGE (16). The weight of the

gonads is divided by the theoretical weight of the fish as determined according to FULTON (15) from the corresponding body length with the coefficient K = 1 ($W = KL^3 \times 10^{-2}$) to obtain the gonad component, which can also be expressed as per cent. In this case,

$$w_{gonads} / w_{total} = GSI = 10^2 \, w_{gonads} / L^3 \qquad [1],$$

where W is the weight in grams and L is the length in cm. This is the isometric GSI, which is unaffected by fluctuations in the empirical weight of the fish. Its relation to GSI's calculated in other ways is fully explained in (6), and the peculiarities of isometric indices are explained in (7).

Gebiet (1)	Periode (6)	Aufteilung (9)	Jahre (13)	Umfang (14)	Basiswerte (18)	Rechnungen (21)	Abb./Tab. (24)
Bornholmsee (2)	1 Jahr (7)	Quartale (10)	1953–55	350–1500 Dorsche/Quartal (15)	Gonadenmassen	Längen-Massebeziehungen (22)	1, 2/2, 3
Gotlandbecken (3)	4 Monate (8)	Reisen, Prob. 0.5–1 Monat (11)	1971–78	300–1000 Dorsche Fangtermin (16)	Reifegrade n. BERNER (20) (19)	Umrechnung m. Masse Bornholmsee (23)	1, 3/2, 3
Arkonasee (4)	1 Jahr	Quartale	1953–55	450–850 Dorsche/Quartal	Gonadenmassen	Längen-Massebeziehungen	4, 5/2, 3
Arkonasee	4 Monate	zumeist (12) Proben/Monat	1981–84	300–900 (17) Dorsche/Monat	Gonadenmassen	Längen-Massebeziehungen	4, 7, 6/2, 3
Mecklenburg. Bucht (5)	4 Monate	zumeist Proben/Monat	1981–84	300–600 Dorsche/Monat	Gonadenmassen	Längen-Massebeziehungen	7, 8/2, 3

Table 1. Description of the samples used for the maturity cycle, and their preparation. Key: 1- region 2- Bornholm Sea 3- Gotland Basin 4- Arkona Sea 5- Mecklenburg Bay 6- period 7- 1 year 8- 4 months 9- intervals 10- quarterly 11- trips, samples/ 0.5-1 month 12- usually samples/ month 13- years 14- size 15- ...codfish/ quarter 16- ...codfish/ catch 17- ...codfish/ month 18- base values 19- gonad weight 20- maturity stage according to BERNER 21- calculations 22- length/weight relations 23- conversion with Bornholm Sea weight 24- Figures/ Tables

Secondly, from the absolute weights of the gonads, percentual changes were derived. Frequently, both the absolute values (Table 2) and the indices (Table 3) give only an inconspicuous reflection of the changes in 50

gonad development over time and the resulting spawning behavior. In order to elaborate more forcefully the major

Gebiet ① Fangtermin		n	a	b	30	40	50	60	70	80	90
Bornholmsee 1953–55 ②											
	20. 3.	287	$5.2 \cdot 10^{-6}$	4.0926	5.8	18.8	46.9	98.6	185.7	320.7	519.4
♂	10. 5.	751	$2.3 \cdot 10^{-5}$	3.6836	6.4	18.6	42.2	82.7	145.9	238.6	368.2
	15. 9.	359	$6.2 \cdot 10^{-6}$	3.8234	0.9	2.1	3.9	6.5	10.1	14.7	20.5
	15. 10.	155	$1.8 \cdot 10^{-5}$	3.5896	1.2	2.6	4.6	7.3	11.0	15.5	21.0
	20. 3.	216	$1.5 \cdot 10^{-7}$	4.9759	3.4	14.4	43.7	108.2	233.0	452.9	813.8
♀	10. 5.	718	$2.9 \cdot 10^{-7}$	5.0001	7.2	30.2	92.1	229.2	495.4	965.8	1740.4
	15. 9.	395	$1.1 \cdot 10^{-6}$	3.5735	2.1	5.8	12.8	24.6	42.7	68.7	104.7
	15. 10.	194	$9.4 \cdot 10^{-7}$	4.1526	1.3	4.2	10.6	22.6	42.9	74.7	121.8
Gotlandbecken 1971–78 ③											
	26. 3.	182	—	—	7.7		59.3		202.7		—
	20. 4.	427	—	—	5.5		48.8		190.2		585.0
	1. 5.	359	—	—	10.7		65.2		185.7		—
♂	13. 5.	410	—	—	14.9		72.8		208.2		518.7
	3. 6.	168	—	—	43.1		61.4		204.0		363.9
	15. 6.	197	—	—	15.6		49.3		94.1		54.3
	26. 3.	115	—	—	2.7		59.2		207.5		837.3
	20. 4.	569	—	—	5.9		79.1		336.2		849.6
	1. 5.	145	—	—	10.3		134.8		476.8		807.3
♀	13. 5.	577	—	—	22.6		145.6		455.8		1048.3
	3. 6.	337	—	—	24.5		154.5		419.2		1006.5
	15. 6.	203	—	—	4.9		97.4		321.2		456.4
Arkonasee 1953–55 ④											
	10. 2.	394	$3.0 \cdot 10^{-8}$	5.5870	0.5	2.7	9.3	25.8	60.9	128.5	248.1
	20. 6.	224	$1.7 \cdot 10^{-6}$	4.6946	1.7	3.6	6.6	10.7	16.3	23.3	32.0
♂	5. 8.	186	$7.1 \cdot 10^{-6}$	3.4289	0.8	2.2	4.7	8.8	15.0	23.7	35.5
	5. 12.	186	$3.5 \cdot 10^{-9}$	5.7471	1.1	5.6	20.2	57.6	139.8	301.1	592.5
	10. 2.	456	$1.0 \cdot 10^{-6}$	4.1839	1.5	5.0	12.7	27.3	52.0	91.0	148.9
	20. 6.	256	$1.5 \cdot 10^{-6}$	4.2088	2.5	8.3	21.2	45.6	87.2	152.9	251.0
♀	5. 8.	189	$7.9 \cdot 10^{-7}$	4.4486	3.3	6.6	11.4	17.8	26.0	36.0	48.1
	3. 12.	255	$3.3 \cdot 10^{-7}$	4.8521	1.4	5.7	17.0	41.1	86.8	165.9	293.8
Arkonasee 1981–84											
	22. 11.	92	$5.2 \cdot 10^{-7}$	4.4501	1.9	7.0	18.9	42.6	84.5		
	15. 12.	129	$1.4 \cdot 10^{-8}$	5.5743	2.3	11.7	40.5	111.8	263.9		
♂	23. 1.	264	$1.3 \cdot 10^{-9}$	6.3556	3.2	19.7	81.4	239.3	690.7		
	1. 2.	120	$1.1 \cdot 10^{-8}$	5.8962	5.5	29.9	111.5	326.6	810.5		
	9. 2.	117	$2.4 \cdot 10^{-11}$	9.0758	0.6	8.4	63.5	332.0	—		
	22. 11.	196	$1.2 \cdot 10^{-7}$	4.8314	1.6	6.4	18.8	45.3	95.5		
	15. 12.	171	$2.6 \cdot 10^{-9}$	5.9165	1.4	7.7	28.9	85.1	211.8		
♀	23. 1.	316	$1.1 \cdot 10^{-9}$	6.2528	1.8	11.0	44.3	138.5	363.0		
	1. 2.	180	$7.4 \cdot 10^{-11}$	6.9734	1.5	11.0	52.0	185.6	543.6		
	9. 2.	183	$8.1 \cdot 10^{-11}$	6.8323	1.0	7.2	32.9	114.2	327.3		
Mecklenburger Bucht 1981–84 ⑤											
	7. 11.	166	$3.9 \cdot 10^{-5}$	3.1704	1.9	4.7	9.5	—	—		
	8. 12.	144	$2.0 \cdot 10^{-7}$	4.8786	3.2	12.9	38.2	92.9	—		
♂	8. 1.	352	$2.2 \cdot 10^{-10}$	6.7078	1.8	12.5	56.0	190.2	534.8		
	7. 2.	141	$6.9 \cdot 10^{-8}$	5.4725	8.4	40.5	137.4	372.8	866.6		
	13. 2.	116	$2.0 \cdot 10^{-10}$	6.5718	1.0	6.8	29.6	98.1	—		
	7. 11.	134	$6.7 \cdot 10^{-6}$	3.6739	1.8	5.1	11.6	—	—	—	
	8. 12.	256	$3.8 \cdot 10^{-10}$	6.3530	0.9	5.7	23.4	74.6	—	—	
♀	8. 1.	538	$9.4 \cdot 10^{-10}$	6.2129	1.4	8.5	33.8	105.1	273.7	627.5	
	7. 2.	135	$5.3 \cdot 10^{-7}$	5.9606	3.4	18.7	70.6	209.3	524.7	1162.9	
	13. 2.	184	$2.5 \cdot 10^{-9}$	5.3139	1.8	8.2	27.0	71.1	—	—	

Table 2. Parameters of the weight-length relation $W = aL^b$ and expected gonad weights (g) for selected lengths (cm). Key: 1- region and dates 2- Bornholm Sea 3- Gotland Basin 4- Arkona Sea 5- Mecklenburg Bay (Read commas as decimal points.)

changes in spawning behavior, the values of one of each sequence of catches-- usually at the beginning of the cyclical development of the gonads-- were set at 100% and the other values were expressed in relation to this

standard. Showing percentual changes of weight in this way is an old and often used method of fishery biology

①	Fangtermin	30	40	50	60	70	80	90
②	**Bornholmsee 1953–55**							
	20. 3.	2.1	2.9	3.8	4.6	5.4	6.3	7.1
	10. 5.	2.4	2.9	3.4	3.8	4.3	4.7	5.1
♂	15. 9.	0.3	0.3	0.3	0.3	0.3	0.3	0.3
	15. 10.	0.4	0.4	0.4	0.3	0.3	0.3	0.3
	20. 3.	1.3	2.3	3.5	5.0	6.8	8.8	11.2
	10. 5.	2.7	4.7	7.4	10.6	14.4	18.9	23.9
♀	15. 9.	0.8	0.9	1.0	1.1	1.2	1.3	1.4
	15. 10.	0.5	0.7	0.8	1.0	1.3	1.5	1.7
③	**Gotlandbecken 1971–78**							
	26. 3.	2.9		4.3		5.9		
	20. 4.	2.0		3.9		5.5		8.0
	1. 5.	4.0		5.2		5.4		—
♂	13. 5.	5.5		5.8		6.1		7.1
	3. 6.	16.0		4.9		5.9		5.0
	15. 6.	5.8		3.9		2.7		0.7
	26. 3.	1.0		4.7		6.0		11.5
	20. 4.	2.2		6.3		9.8		11.7
	1. 5.	3.8		12.4		13.9		11.1
♀	13. 5.	8.4		11.6		13.3		14.4
	3. 6.	9.1		12.4		12.2		13.8
	15. 6.	1.8		7.8		9.4		6.3
④	**Arkonasee 1953–55**							
	10. 2.	0.2	0.4	0.7	1.2	1.8	2.5	3.4
	20. 6.	0.6	0.6	0.5	0.5	0.5	0.5	0.4
♂	5. 8.	0.3	0.3	0.4	0.4	0.4	0.5	0.5
	5. 12.	0.4	0.9	1.6	2.7	4.1	5.9	8.1
	10. 2.	0.6	0.8	1.0	1.3	1.5	1.8	2.0
	20. 6.	0.9	1.3	1.7	2.1	2.5	3.0	3.4
♀	5. 8.	1.2	1.0	0.9	0.8	0.8	0.7	0.7
	5. 12.	0.5	0.9	1.4	1.9	2.5	3.2	4.0
	Arkonasee 1981–84							
	22. 11.	0.7	1.1	1.5	2.0	2.5		
	15. 12.	0.9	1.8	3.2	5.2	7.7		
♂	23. 1.	1.2	3.1	6.5	12.0	20.1		
	1. 2.	2.0	4.7	8.9	15.1	23.6		
	9. 2.	0.2	1.3	5.1	15.4	—		
	22. 11.	0.6	1.0	1.5	2.1	2.8		
	15. 12.	0.5	1.2	2.3	3.9	6.2		
♀	23. 1.	0.7	1.7	3.5	6.4	10.6		
	1. 2.	0.6	1.7	4.2	8.6	15.8		
	9. 2.	0.4	1.1	2.6	5.3	9.5		
⑤	**Mecklenburger Bucht 1981–84**							
	7. 11.	0.7	0.7	0.8	—	—	—	
	8. 12.	1.2	2.0	3.1	4.3	—	—	
♂	8. 1.	0.7	2.0	4.5	8.8	15.6	—	
	7. 2.	3.1	6.3	11.0	17.3	25.3	—	
	13. 2.	0.4	1.1	2.4	4.5	—	—	
	7. 11.	0.7	0.8	0.9	—	—	—	
	8. 12.	0.3	0.9	1.9	3.5	—	—	
♀	8. 1.	0.5	1.3	2.7	4.9	8.0	12.3	
	7. 2.	1.3	2.9	5.6	9.7	15.3	22.7	
	13. 2.	0.7	1.3	2.2	3.3	—	—	

Table 3. Isometric gonadosomatic indices (GSI's) for selected lengths (cm), expressed as per cent. Key: 1- sampling dates 2- Bornholm Sea 3- Gotland Basin 4- Arkona Sea 5- Mecklenburg Bay (Read commas as decimal points.)

for describing cyclical processes. In the present case, then, the curves of the sampling dates over all body lengths (Figures 1, 4, and 7) yield percentual curves for the different body lengths over the entire year or a part

of the year (Figures 2, 3, 5, 6, and 8). The dates of the catches taken as standards can be seen from the figures.

The percentages can be calculated either from the indices in Table 3, or-- with somewhat greater accuracy because the values are not rounded-- from the absolute weights of the gonads in Table 2. When comparing body lengths, sexes, or regions, the scope of the percentual values will depend largely on the level of the weights taken as 100%, and as a rule, it could be very different if another sampling date were chosen as the standard. For this reason, the overall levels of the percentual values will be of minor interest for our purpose; what is important is the relative increase or decrease of each percentual curve.

It should also be pointed out that the quarterly 51
assessments should be taken with the calculation of a weighted temporal average at the following dates:

	Bornholm Sea	Arkona Sea
1st quarter	20.3	10.2
2nd "	10.5	20.6
3rd "	15.9	5.8
4th "	15.10	5.12

All sampling dates are listed in Tables 2 and 3 and 51
plotted on the figures according to their distribution in time. The distribution of individual samples from the 1950's can be seen in (6).

The Southern Gotland Basin was treated differently from the other regions, insofar as no records of gonad weights were available, but only maturity stages according to BERNER or MAIER (4). In order to derive approximate values for the weight of the gonads from these data, we used the mean weights of the gonads of the corresponding sex, maturity stage, and body length in the Bornholm Basin (6). These values were then further processed as usual.

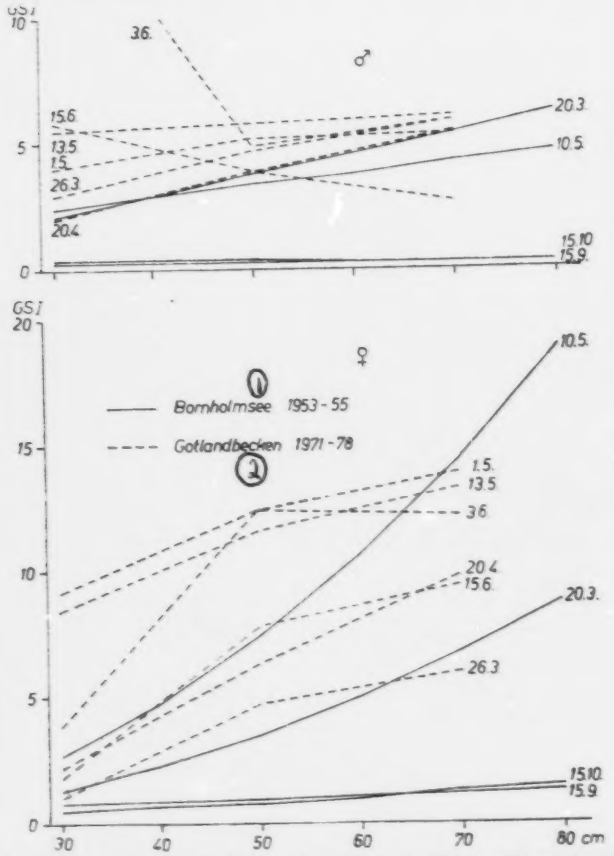

Figure 1. Gonadosomatic indices for Bornholm Sea from 1953 to 1955 and for Gotland Basin from 1971 to 1978. Key: 1- Bornholm Sea 2- Gotland Basin

Already known elements of the spawning behavior of cod in the Baltic

Since many authors have discussed in some fashion the spawning behavior of cod in the Baltic, a comprehensive survey of the literature can not be given here. However, certain authors should be mentioned who have studied the topic in depth and contributed new knowledge or else provided good reviews of what is known.

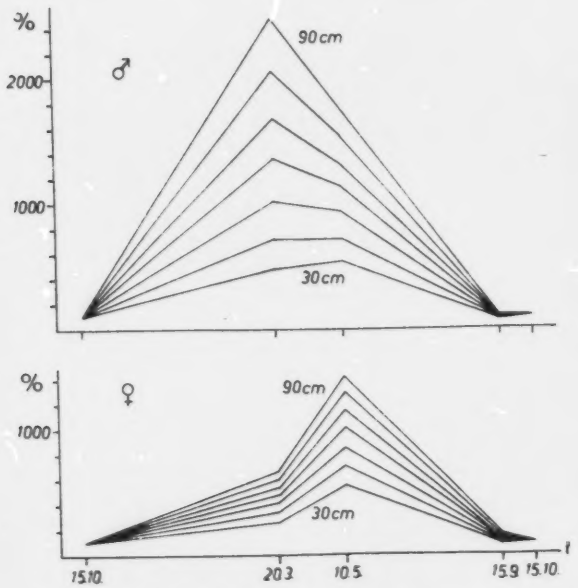

Figure 2. Annual percentual changes of the weight of the gonads in the Bornholm Sea from 1953 to 1955. Key: 't' = date.

First of all, KAENDLER should be mentioned, who contributed reliable data on basic known facts and in particular, discovered the fall-spawning cod of the 52
Bornholm Basin (17, 18). Of course, also MEYER (19) studied spawning cod and described such phenomena as the rejuvenation of the shoals during the spawning period and

the qualitative changes associated with spawning. CHRZAN gave the first fully detailed description of the different behavior of males and females on the Baltic spawning grounds east of Bornholm, and gave gonadosomatic indices (12, 11). BERNER (4, 3) discussed the current

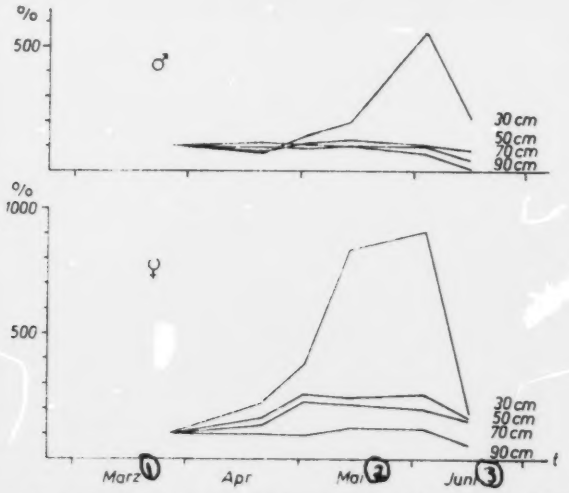

Figure 3. Percentual changes of the weight of the gonads over a period of four months in the Gotland Basin, in 1971 to 1978.
Key: 1- March 2- May 3- June 't' = date

findings in 1960 and 1958, supported some of these findings with new material, converted MAIER's maturity scale for all fishes into a scale for cod, and contributed, e.g., accurate determinations of the weight of the gonads for the cod around Bornholm, highlighting the much greater relative fertility of females compared to males. The basic data compiled in this study were later reworked with an improved method (6, 7) and form the basis of statements regarding the 1950's. In 1957, BERNER and SCHEMAINDA (2) described the pelagic spawning concentrations in the Bornholm Basin and their hydrographic

causes. In 1970, BIRJUKOV (10) published a monograph on cod in the Baltic including a lengthy description of the spawning behavior of cod from Kiel Bay to the Gotland Basin based on the literature and on the author's own investigations. This work presents essentially the current state of knowledge. The more recent investigations of the 50% maturity length of the sexes and their spatial distribution by THUROW (1970) (23) for Kiel Bay and by BERNER and VASKE 1981 (5) for Mecklenburg Bay and the adjacent regions essentially provide a better foundation for previously known facts such as the lower 50% maturity length of the cod east of Bornholm, and cast new light upon questions of the variable mixture of adult and juvenile fish depending on depth.

The following items, then, may be accepted as fundamental:

--the spawning seasons of the different codfish stocks in the Baltic

--the main spawning grounds, and spawning depths in relation to salinity and oxygen saturation

--the proportions of adult and juvenile fish in relation to depth

--the proportions of males and females in relation to depth

--the lower 50% maturity length of cod east of Bornholm compared to those west of Bornholm (The cod east of Bornholm become sexually mature at a lesser length.)

--the lower 50% maturity length of males compared to females (Males become sexually mature at a lesser length.)
--the greater fertility of females compared to males
--the more rapid ripening of males at the beginning of the spawning period
--the earlier arrival of the males at the spawning grounds
--the fact that the males remain at the spawning grounds longer before they are fully spent
--the lower mean age of the male stock resulting from their longer stay at the intensively fished spawning grounds
--the excess of males in the smallest length-group resulting from their earlier sexual maturation
--the fact that larger fish finish spawning at the beginning of the spawning period, whereas smaller fish and those spawning for the first time finish at the end of the period
--the increase in relative fertility with increasing body length.

Some of these findings are relative and not fixed for all times, some are even fluctuating and incomplete. For example, the temporal sequence of large and small spawners has hardly yet been studied separately for male and female cod. Consequently, in what follows, new

discoveries and deviations from known patterns are discussed. More often, known findings are confirmed.

Results for Bornholm Basin and Gotland Basin

For Bornholm Sea cod, Table 2 conveys an actual overview of the major cyclical changes of the weight of the gonads during the year, but also of the growth of the gonads with progressive growth of the fish, and of the differences between males and females in this regard. Evidently the females produce a greater bulk of gonads compared to the males and do not attain as extensive retrogression of the gonads during the resting stages, so that those over 40 cm almost always exhibit higher mean gonad weights. In the Gotland Basin, cyclical changes are less distinct, because only four months of the cod season were sampled, instead of the full yearly cycle.

To obtain comparable values for the different body lengths, the relative weights of the gonads expressed as isometric GSI's according to (1) are shown in Table 3 and plotted in Figure 1 for both sexes and both regions. Here too the females over 40 cm show distinctly higher indices. Also, there is usually a more or less marked rise in the relative weights of the gonads with increasing length. Up to 60 cm, the indices at comparable intervals in the Gotland Basin are higher than in the Bornholm Sea. Since empirical gonad weights were not

available for the Gotland Basin, this result will not be discussed further, and remains questionable.

Figure 2 shows that in the Bornholm Sea the percentual rise and decline of the weights of the gonads of both sexes over the year trace an unusually regular pattern. Everything indicates that large and small cod have a common spawning season every year. The relatively low concentrations of fall-spawning cod in the Bornholm Basin described by KAENDLER (17) are not observable in this material, especially since the fall material listed here was not caught on the spawning grounds. At the same time, this fact shows that not necessarily all processes of spawning behavior are reflected.

Comparison of the sexes reveals the seasonally late maximum of the females. Evidently females of all comparable lengths attain their maximal gonad weight and their spawning peak at a later date than males of the same size. This phenomenon has been known from the elaboration of spawning biology by means of maturity scales at least since CHRZAN (12). A shifting of the maximum weight of the gonads within the lengths cited is recognizable only among males: Here we see that smaller males ripen later than larger males, so that those measuring 30 cm finally reach their maximum gonad weight, like the females, on 10.5 instead of 20.3. Investigations of maturity stages indicate that we should expect a similar development after 10.5 among females, but because

of the temporal gap which follows in our samples, it is not established. However, we can see the faster gonad development of the large females after 15.10 in a new maturity cycle.

The material collected over a period of four months from the spawning fishery in the Southern Gotland Basin was used to supplement the findings for the Bornholm Sea. Although the sampling dates are closer together and cover only the pre-spawning and spawning periods, this material is less uniform than in the Bornholm Sea, because almost every sampling date corresponds to a different year, and no empirical gonad weights are available. It is clear from Figure 3 that the weight of 53
the gonads of males from 50 to 90 cm long hardly changes from the end of March to the beginning of June, while that of the corresponding females hardly changes-- after an initial increase staggered according to body lengths-- from the beginning of May to the beginning of June. This corresponds with the mean maturity stage of the spawning population, which remains steady through the main spawning phase, whether because partially spent males stay for a long time on the spawning grounds, or whether the typical breakdown of spawning stages in both sexes is kept constant at this time by the steady arrival and departure of ripening or spent fish.

In the middle of June a decline of the weights of the gonads becomes perceptible in both sexes, and it is

sharper in large fish than in small fish. This is evidence of the fact that on average, the large cod are spawned out earlier. That they begin spawning earlier is indicated, in addition to the staggered rise of the values for females in April, by the late start of the fish with a length of 30 cm, with males of this length not reaching their maximum gonad weight until early June. The first-time spawners making up this group are markedly late spawners. Comparison with females 30 cm long seems to indicate that the small males appear for a relatively short time. According to BERNER and VASKE (5) the females become sexually mature, on average, only at a greater body length than males. This is shown also by the present results. According to Figure 1 and Table 3, on 3.6 males 30 cm long have a much higher GSI (16.0) than females (9.1). At the same time, this comparison makes it clear that the height of the maxima on the percentual curves can be deceptive, because it depends on the standard, but that the rising or falling trends remain.

To summarize, previous and new discoveries yield the following findings for the codfish spawning in the deep basins east of Bornholm:

1. Apart from certain fall-spawning codfish known from the literature, this fish shows a very uniform spawning cycle which is characterized by a main spawning period lasting two to three months from April to July, during which the composition of maturity stages in the spawning

population changes little, because of arrivals and departures.

2. Unlike the composition of maturity stages, the size composition of the spawning population changes during the main spawning period. Among both males and females, spawning is initiated preferentially by large and medium-length fish, while the small first-time spawners are the last to search out the spawning population, and finish spawning relatively late. Especially in the case of the males, it must be assumed that the large individuals remain on the spawning grounds considerably longer than the small fish.

3. The main spawning period begins later for females than for males of the same size. It ends at approximately the same time for both, because the females become spent faster than the males.

4. On average, the female stock of spawners is older than the male stock and greater in length, because the females, with their later maturation and their shorter stay on the spawning grounds, are not fished as intensively.

Results for Arkona Sea

For the codfish in the Arkona Sea, there is a four-month study for the years from 1981 to 1984, and a year-round study for 1953-1955. It is striking that the dates of 1.2 and 23.1 1981-1984 exhibit high GSI's such as correspond with those of Mecklenburg Bay (Figure 7)

but were never reached in the Arkona Sea from 1953 to 1955, although there was a sampling at a corresponding

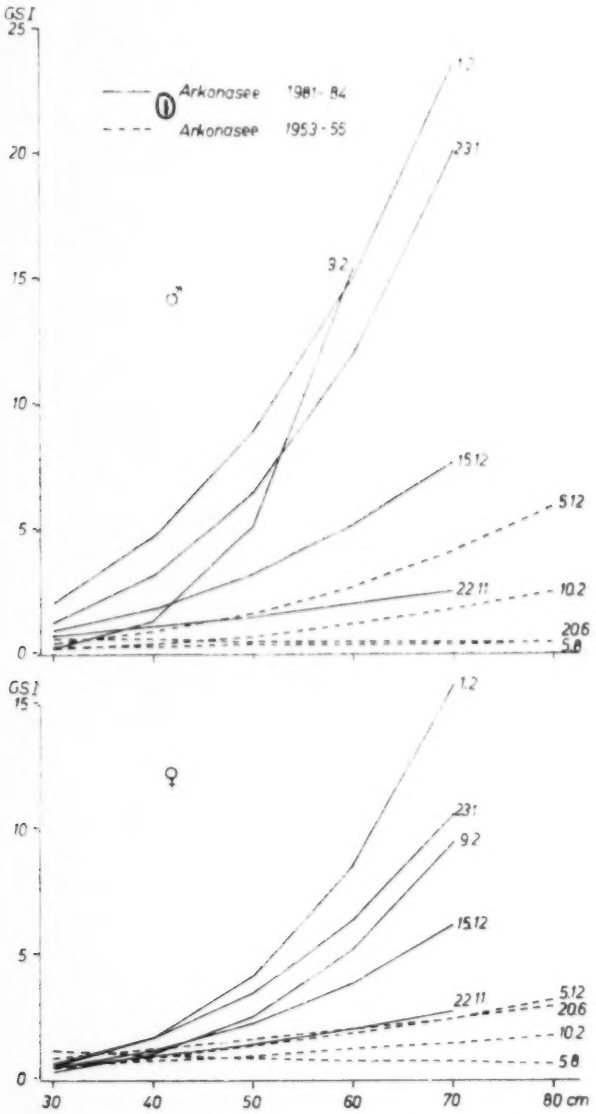

Figure 4. Gonadosomatic indices for the Arkona Sea in 1953-1955 and 1981-1984. Key: 1- Arkona Sea

time on 10.2 (Figure 4). Apparently the main reason is that in 1953-1955 the indices declined already from 5.12 to 10.2, and not only in February as in the eighties. Compare the percentual values in this regard.

The year-round material for 1953-1955 is presented in Figure 5. In view of the fact that some of the curves on this chart have two peaks, it seemed advisable to set the values at 100% between the two peaks, viz., on 10.2 or 5.8. Given the levels resulting for all values, 10.2 turned out to be somewhat more favorable. This alters the course of the curve on the stretch from 5.12 to 10.2, which is comparable in time with Figures 6, 8, and 2, with respect to the position of the 100% point. If the values for the weight of the gonads on 5.12 were set at 100%, this would yield the following values, which are suitable for comparison, for 10.2:

	males (%)	Females (%)
30 cm	45	107
40 cm	48	88
50 cm	46	75
60 cm	45	66
70 cm	44	60
80 cm	43	55
90 cm	42	51

Accordingly, in the material from the 1950's, from December to February, we find a constant decrease of the weight of the gonads to less than half for the males, and increasing reductions, down to 51%, for females starting from 40 cm-- results which do not correspond, or correspond only to a limited extent, with those of other years and regions. A similar decline is expressed also in Figure 5 in spite of the different standard, and confirms that in each case the changes in the direction of the

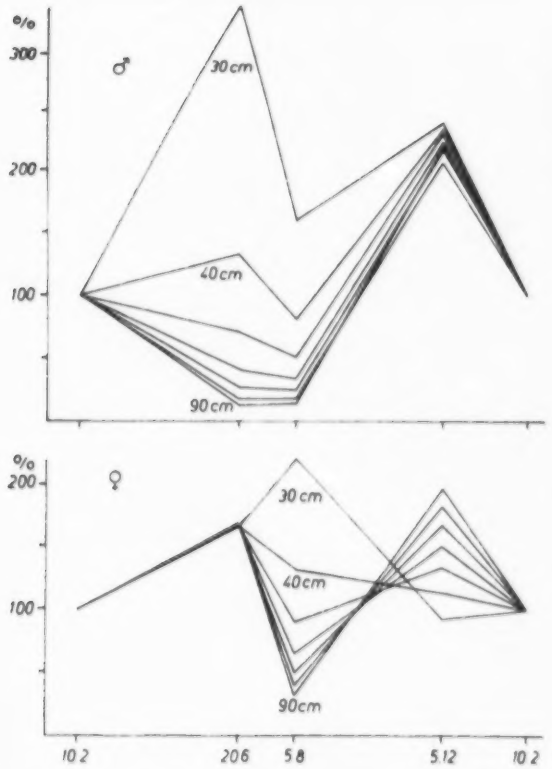

Figure 5. Yearly percentual changes of the weight of the gonads for the Arkona Sea from 1953 to 1955.

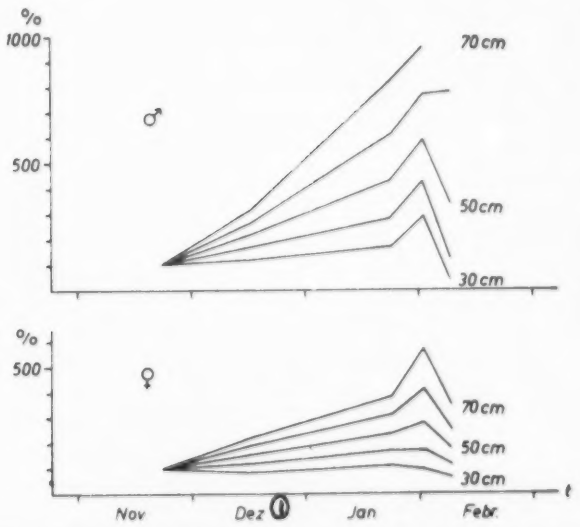

Figure 6. Percentual changes of the weight of the gonads over a period of four months in the Arkona Sea from 1981 to 1984 Key: 1- Dec.

percentual curves are comparable. These results indicate that the spawning behavior of cod in the Arkona Sea is 54
different from that of other stocks, or that it exhibits more distinctly a peculiarity of mixed stocks.

Let us begin with the spawned out fish of the 1950's. Apart from a few stragglers especially among females 30-40 cm long spawning for the first time, the 'spawned out' condition is essentially attained by both sexes on 5.8. Between 5.8 and 5.12 a new cycle begins, generally marked by an increase of the weight of the gonads. As a rule, larger fish are spent earlier and begin to rebuild their gonad weight earlier than smaller fish, so that they are already farther advanced in their development on 15.12. This is expressed, especially for females, in Figure 5. According to the GSI values, the ripening continues until 5.12 in the same fashion as in the same area (Figure 4) and in Mecklenburg Bay (Figure 7) in the eighties; then the differences begin, insofar as in the fifties, a further increase in gonad weight which appears in itself very natural at this time (in the pre-spawning period) is interrupted, and continues only in the second quarter at a lower level, particularly among females. This is shown very clearly in Figure 5. Everything indicates that in the fourth quarter, cod at a different stage of maturity, and consequently with a different spawning season were caught than in the first quarter. We shall return to this peculiarity.

The weight of the gonads of females rises again very uniformly from 10.2 to 20.6 and peaks on 20.6; sometimes this peak is also the maximum for the year, but its indices (Table 4) are far removed from the values of the eighties. Hereafter the gonad weight of the largest females falls most rapidly and most abruptly, whereas the smallest females exhibit a maximum only as late as 5.8. By 10.2 the males have probably already started to spawn, and their gonad weight decreases distinctly until 20.6. Only the stragglers-- primarily first-time spawners 30 cm long-- can still show a marked rise in the weight of the gonads on 20.6. Apart from these, the GSI for the males is highest on 5.12. From 20.6 to 5.8 the weights of the gonads decrease in almost all length-groups; only in males 90 cm long, there are already slight indications of the start of the new cycle.

Let us turn now to the results for 1981-1984. The indices follow a similar course to that of codfish in the Bornholm Sea, but with each phase considerably earlier. Female codfish 70 cm long in the Arkona Sea have already attained on 1.2 a GSI similar to that exhibited by the females in the Bornholm Sea on 10.5, while the smaller fish in the Arkona Sea on 10.5 are still far behind those in the Bornholm Sea in the development of their gonads. The males are more advanced in their gonad development than the females. On 23.1 and 1.2 they attain indices distinctly exceeding those of the females on 1.2.

Figure 6, if we take the November values as 100%, shows a regular increase of the weight of the gonads in both sexes until the end of January. Only females 30 cm long are hardly sexually mature, and their gonad weights remain at approximately the same level. The earlier maturation of the males is clear. It is also clear that starting in November, and especially starting in the middle of December, the males ripen at a faster pace than females. At the beginning of February, a certain retardation of the increase in the weight of the gonads becomes noticeable in the largest males. At first glance, this could indicate that the first fish are beginning to be spawned out. A similar stage in females is definitely not noticeable by the beginning of February; rather, the gonad weight of the largest females increases considerably precisely at this time, while the smaller females can be seen to be ripening more slowly and finally becoming increasingly interspersed with juvenile fish. A main spawning period such as was expressed especially in the material from the Gotland Basin has probably not yet been reached in the Arkona Sea in early February, but there seem to be indications of it at this time among the large males. Until early February, there are differences from the material of the fifties with respect to the course of the curves and the height of the index values, but with the percentual values of February 9, as in the fifties, the gonad weights recede, albeit definitely not

to such low indices as in 1953-1955. Yet there are still indications also in 1981-1984 of the presence in the Arkona Sea of spawning or pre-spawning shoals at different maturity stages. Since fishing depths and water temperatures, but also the mix of the stock can always play a role, the grasp by the fishery of a phenomenon like the formation of pre-spawning shoals at different stages of development in different years will vary. It seems highly unlikely that the results of the fifties were accidental.

Gebiet/Monat ①	1976	1977	1978	Mittel	1979	1980	1981	1982	Mittel
Arkonasee ②									
März/April t ④	346	120	260	242	336	167	319	176	250
Juni/Juli t ⑤	288	64	177	176	314	313	333	558	430
März/April %	55	65	59	58	52	35	37	24	37
Juni/Juli %	45	35	41	42	48	65	63	76	63
Gebiet/Monat	1976	1977	1978	1979	Mittel ⑥	1980	1981	1982	Mittel
Mecklenburger Bucht ③									
März/April t	203	104	182	54	136	62	107	103	91
Juni/Juli t	18	30	63	25	34	63	110	165	113
März/April %	92	78	74	68	80	50	49	38	45
Juni/Juli %	8	22	26	32	20	50	51	62	55

Table 4. Relative productiveness of codfish catches of the 17 m cutter class in the Arkona Sea and Mecklenburg Bay. Key: 1- region/ month 2- Arkona Sea 3- Mecklenburg Bay 4- March/ April 5- June/ July 6- mean

If we consider the racial differentiation of the commercial codfish stock in the Arkona Sea as shown by the number of fin-rays in the second dorsal fin (D_2), it is clear that from the 1950's until about 1979 this was always a highly mixed stock of Gadus morhua callarias L. and Gadus morhua morhua L. Starting with the 1976 generation, the Baltic callarias prevailed increasingly in the Arkona Sea and the proportion of Belt Sea cod receded (8). 55

In its own regions the Belt Sea cod spawns chiefly from February to April, and the Baltic cod from April to July. Also when these racially differentiated subgroups of cod in mixed stocks form their own spawning populations at their characteristic spawning seasons, this should be observable in the yields of the cod fishery. To this end, the catches of the commercial cod fishery for March/ April and June/ July are compiled in Table 4. Here, especially the June/ July yields should establish the presence of spawning Baltic cod quite reliably, since after the end of the spawning period, the codfish are so dispersed that practically no landings were recorded. Compiling the annual values reveals that the June/ July catches made up 42% in the Arkona Sea in 1976-78 and rose to 63% starting in 1979, whereas the March/ April catches in the same years fell from 58 to 37%. Thus, the ratio of the June/ July yields not only corroborates the findings from the 1950's of the late spawning concentrations of Baltic cod before 1979, but also furnishes a clear and temporally precise reflection of the increase of Baltic cod in the spawning stock starting in 1979/ 80. A disadvantage of the biological material from the eighties is that it breaks off too early in the year.

Accordingly, we must essentially assume that in mixed stocks of cod in the Baltic, the Belt Sea and the Baltic groups form their own spawning populations at

their respective characteristic spawning times, and that for this reason a certain degree of isolation of their pre-spawning and spawning shoals is possible and probable. This was clearly recognizable in the material from the fifties from the two peaks of many of the curves, but apparently it also contributed to the unusually low gonad weights, insofar as the peak spawning times of both populations were not included together in any single quarter.

The material from the eighties only approximately reflects the spawning culmination of the Belt Sea cod. It is remarkable in this connection that at such an early date the Baltic cod, in spite of its abundant presence in the region, has so little influence upon the index values of the gonads, and reduces them so little, particularly for fish over 50 cm long. At this point we may recall another phenomenon which was discovered recently in growth studies (9) and is supported by correspondingly high D_2-values. Starting at about December in the Arkona Sea, normally there are increasing catches of large codfish resembling those in the Danish Belt Sea and the Kattegat. It is assumed that these fish sometimes undertake a feeding migration shortly before their own spawning season, by following the shoals of spring herring spawning near Ruegen. This could have a decisive influence upon the high gonad indices for large cod.

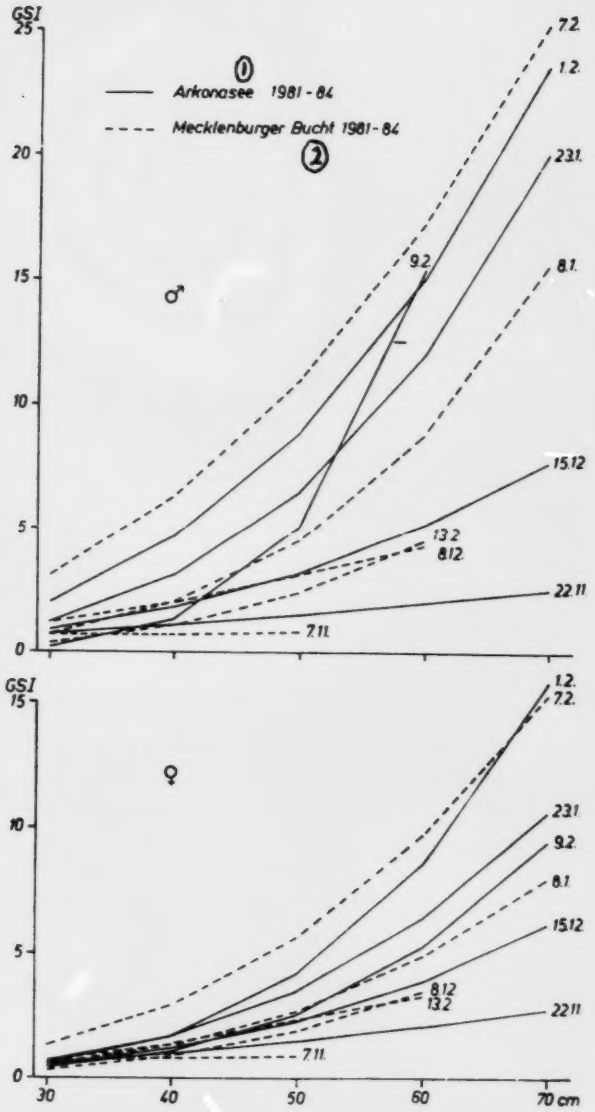

Figure 7. Gonadosomatic indices for Mecklenburg Bay and the Arkona Sea from 1981 to 1984 Key: 1- Arkona Sea 2- Mecklenburg Bay

In summary, we can make the following statements:

1. Points 2-4 listed for the codfish in the Bornholm Sea and the Gotland Sea apply essentially also to the mixed components in the Arkona Sea: i.e., larger fish of the same sex spawn earlier than the smaller fish; and males

start spawning earlier in the year than females of the same size, and then finish spawning more slowly; and the female stock at the spawning grounds is older than the male stock because of the earlier sexual maturation of the males and their earlier ripeness for spawning, and because of the more intensive fishing which results.

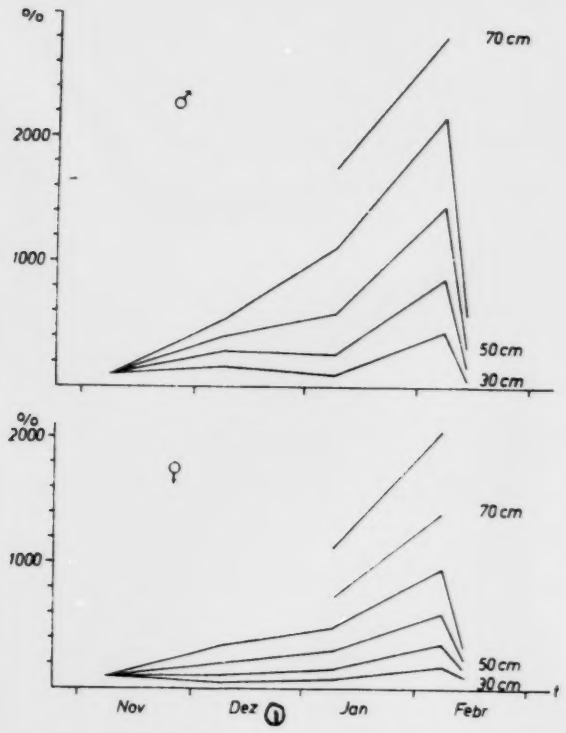

Figure 8. Percentual changes in the weight of the gonads over a period of four months in Mecklenburg Bay from 1981 to 1984 Key: 1- Dec.

2. The Arkona Sea stock is differentiated from the eastern cod as a typical mixed stock by the length of the spawning period and the uneven level of gonad development. Everything indicates that the components of the mixture-- Baltic cod (Gadus morhua callarias) and Belt 56

Sea cod (Gadus morhua morhua)-- each maintain their own spawning cycle at their own times and form separate spawning populations. This leads to an extended spawning season from February to July. Since 1979, the patterns of spawning and catches of spawning cod have changed because of the suppression of the Belt Sea cod.

3. For several years, starting around December, mainly large codfish have been found in the Arkona Sea. These fish resemble the cod of the Kattegat in their growth and racial differentiation; they probably migrate to the Arkona Sea with the spring herring spawning near Ruegen, and exhibit the advanced gonad development of Belt Sea cod.

Results for Mecklenburg Bay

For the codfish in Mecklenburg Bay, only results from the years 1981-1984 are available. From Tables 2 and 3 and Figure 8 we see that the gonad weights and the indices for comparable length-groups and intervals of time up to 7.2 differ relatively little from those of the Arkona Sea cod. Unfortunately, there are hardly any more gonad weights available for later dates; however, a sample of 13.2 shows a decline to values similar to those of 8.12. The reduction of the gonad indices is considerable, exceeding even the reduction from the fourth to the first quarter in the Arkona Sea.

Based on experience, in previous years we should have expected the main spawning period to begin in February and to end in the second half of April. As Table 4 shows, the component of the June/ July yields increased from 20 to 55% starting in 1980; according to the arguments already set forth in connection with the cod in the Arkona Sea, this is a very reliable indication that the spawning season was extended by the late-spawning Baltic-cod components in a mixed stock of Baltic and Belt Sea cod. In fact, also fin-ray counts of the second dorsal fin indicate that the Baltic cod has spread more to the west in recent years, beginning with the generation of 1976 (8). As a result, since about 1980, the commercial codfish stock in Mecklenburg Bay has become a typical mixed stock, as was the case especially in earlier years in the Arkona Sea. The different gonad indices of the catches on 7.2 and 13.2 indicate a differentiation of spawning and pre-spawning shoals.

Figure 8 shows the percentual growth of the gonads in Mecklenburg Bay from November to February. It shows continuous gonad development, accelerating in January, to the beginning of February-- with some tendencies to slower development in females 30 cm long, and some fluctuations among males 30 cm long. Among 30 cm Belt Sea codfish in Mecklenburg Bay, the females are hardly yet sexually mature, and only a small proportion of the males are mature (5). In the middle of February

the continuous gonad development is interrupted by codfish at about the same stage as was found in early December, which probably comprise predominantly the late-spawning Baltic cod. To summarize:

1. Points 2-4 of the findings listed for cod in the Bornholm Sea and the Gotland Sea, applied consistently to the component spawning populations of mixed stock, are valid also for the cod of Mecklenburg Bay.
2. For Mecklenburg Bay, with its previously mostly pure stock of Belt Sea cod, until 1979 a main spawning period of approximately two months' duration was normal, from the middle of February to the end of April. Starting in 1980 an increased admixture of Baltic cod led to an extension of the spawning season into July, and to the formation of separate spawning populations of the respective races of cod. Since then, the stock of Mecklenburg Bay has been a typical mixed stock.

Summary

The investigation of gonad development by means of fitted curves of the weights of the gonads has confirmed some previously known facts regarding the spawning cycle of cod in the Baltic. The earlier sexual maturity and spawning ripeness of males compared to females of the same spawning population found some form of expression in every region. It was shown that within the same spawning population, the larger individuals of both sexes initiate

the spawning, while the small fish and first-time spawners are the last to spawn during the typical season for that population.

It seems to be a new discovery that in mixed stocks of Baltic (Gadus morhua callarias) and Belt Sea cod (Gadus morhua morhua) the spawning season is extended because of the different spawning times of the two components. It appears that both groups form their own spawning populations, resulting in racially differentiated pre-spawning and spawning shoals.

Mixed stocks of codfish are present in the Arkona Sea and Mecklenburg Bay. In both of these stocks the proportion of Baltic cod has increased since 1980, altering the times of the intensive spawning season and catches of spawning cod. The earlier spawning period of the Belt Sea cod and the later spawning of Baltic cod provide an excellent explanation of SICK's (21) discovery from genotypes that in the Arkona Sea there is a mechanical mixture of the two races, rather than interbreeding.

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